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EMBRYOLOGY.[1]

Cleavage and the Formation of Organs.—An important addition to the accumulations of experimental embryology has been recently made by Oscar Hertwig[2] in the hope of clearing up the fogs that envelop the important subject of the relations of the cells of a cleaving ovum to the subsequently formed organs of the adult.

While His, Roux and Weismann have seen in the ovum or germ a preformation of parts or organs and looked upon the cleavage cells as different in quality from the first, regarding the process of embryo formation as an evolution (in the old sense), Driesch and Hertwig, from experimental studies, now regard the ovum as *isotropic*, its first cells are qualitively alike, the embryology is an epiginetic formation of organs. The process is one of inter-relation of the cleavage cells.

In the present paper the author describes a long series of experiments made upon frogs' eggs and applies them to the overthrow of Roux's main position, meeting that investigator upon his own grounds.

The methods used are: the compressing of the eggs between glass slides placed horizontally, vertically or inclined; the compressing of the eggs by drawing them into narrow glass tubes placed horizontally or vertically; the partial separation of the first two cleavage cells (in the Triton) by means of a loop of fibre from a cocoon tied about the the egg; the injury of one of the first two cells by the insertion of a needle; and the same result by the use of an electric current, continuous or interrupted.

We will first give some of the chief facts obtained by each method and then the author's conclusions.

When the eggs lie in the normal position upon a glass slide but are compressed by the slide that rests upon them so as to be no longer spherical but considerably flattened, the main axis from the black to the light pole being thus made the shorter, by a third or a fourth, the eggs cleave in an abnormal manner. The third plane is not horizontal but more nearly vertical so that the first eight cells form a bilaterally symmetrical set of four on each side the second cleavage plane. Again, if the pressure is exerted upon the sides of the egg, which is done by plac-

[1]Edited by E. A. Andrews, Baltimore, Md., to whom communications may be sent.

[2]Archiv fr Mik. Anatomie. 42. 22 Dezember, 1893, pps. 662–794, Pls. 39–44.

ing the slide vertical and allowing the eggs to take up their normal position before the second slide is pressed upon them, the cleavage is abnormal. The second plane is not a vertical one but is horizontal so that two black-pole cells and two light-pole cells are formed. The two former cells are very small and divide up by somewhat vertical planes parallel to the first. Thus the second, normal, plane remains long absent. When the plates are inclined to 45° a still different modification of cleavage results.

The eggs that are drawn into narrow tubes are distorted into cylindrical or barrel-shaped masses that cleave abnormally. When the tube rests horizontally the first plane is vertical or normal but always at right angles to the axis of the tube, the second is normal, that is, at right angles to the first, but the third is also vertical and not horizontal: the fourth is horizontal.

When the tube is placed vertically the black part of the egg is uppermost and the cleavage is again altered by the pressure of the tube. The first plane is oblique and variable, but divides off a smaller upper cell from a larger lower cell.

All these abnormal modes of cleavage may, the author maintains, be explained upon his principle that the cleavage plane is at right angles to the axis of the nuclear spindle and that the position of the spindle-axis is dependant upon the shape and character of the protoplasm about it; the poles of the spindle lie in the directions of the greatest masses of protoplasm. Pressure acts by changing the shape of the protoplasmic mass and thus inducing a new direction for the nuclear spindles. That in the frog different forms of cleavage result when the egg is pressed from the side or from above downward is to be explained by the quality of the protoplasmic masses, the nature of the protoplasm, admixture of yolk, etc. being a factor as well as its mass in regulating the direction of the nuclear spindle. This explanation is thus more fundamental than the principles of surface tension and rectangular intersections of cleavage planes, which follow in part from this action of mass upon nuclear arrangement.

If the eggs remain under pressure between the plates or in the tubes they continue to develop, form gastrulas and, in some cases, larvæ. This furnishes a good means of confirming the contention of Pfluger and of Roux that the medullary folds really are formed upon that side of the egg which is at first the light colored lower side though they normally appear upon the upper side and would hence be naturally regarded as formed from the black or animal-pole side.

Between horizontal glass plates the gastrulation takes place so that the crescentic blastopore lip appears upon the edge of the lower side of the disk-shaped egg, at any point of this periphery. It then travels, in some way not observed, across the lower, flat surface, and closes at a point of the periphery diametrically opposite to that whence it started. Now in sections it is found that the yolk mass is at first at the end near the first position of the blastopore, then shifting, lies at the other end.

If the egg were free and not held fast by the pressing plates this shifting of the center of gravity would tend to revolve the egg so that its lighter colored part would become uppermost. Meanwhile the head fold and medullary folds come in near and along the region traversed by the blastopore (they are found upon the flat *under* side of the compressed egg) and hence would normally appear upon the upper side if this rolling of the egg took place.

Passing over some other interesting observations we may mention those made upon eggs that were forced to develop up-side-down. This was done by turning them over, under pressure, after the first or second cleavages. The light colored part of the egg thus remains uppermost The eggs develop normally at first but finally when gastrulation begins the blastopore is irregular in shape and the yolk is asymetrically distributed so that very imperfect and monstrous gastrulas result.

An attempt to separate the first two cells of tritons by drawing a loop of fine silk about the constriction between them did not succeed, since the two cells remained connected by an isthmus. Yet as they were held partly apart some curious modifications in the development resulted. The results are, however, very diverse. Each cell may cleave and a dumbell-shaped blastula result and eventually a monstrous embryo formed half upon one side of the thread, half upon the other or chiefly upon one side and partly upon the other. The nervous system may be outlined altogether upon one of the parts kept apart by the thread.

What may be considered the most important part of the paper is that treating of Hertwig's repetition of Roux's experiments upon the development of frogs eggs in which one of the first two cells is destroyed or injured by needle thrusts.

Such eggs continue to develop, but produce abnormal embryos. Roux maintained that the uninjured half of the egg formed a half blastula, half-gastrula, etc. Hertwig claims that this is not the case and figures many sections that support his claim very convincingly.

The development of the uninjured half of the egg is not as it would be in an entire egg but is so modified by the presence of a partly dead mass adjacent to it that it produces what may be called rather an abnormal blastula with an inclusion of inactive or dead yolk than in any sense a half-blastula.

Later, abnormal gastrulas are formed. These, however, are not *Semigastrulæ laterales*, *anteriores* or *posteriores* as Roux describes, but gastrulæ checked and distorted in their formation.

It seems, moreover, that only the presence of the inactive or dead yolk of the injured cell prevents the living cell from developing into a complete small gastrula as in the echinoderm experiments of Driesch. This dead or injured mass remains intimately attached to the live cell and hence is incorporated as a part of the embryo which it modifies somewhat as the yolk of a meroblastic egg modifies the part that forms the embryo.

Some eggs develop even the medullary folds and the notochord and form parts of larvæ. These are, however, very incomplete and also much varied in character; since, apparently, the injured cell is killed, coagulated, only in the part near the needle hole and may become, elsewhere, utilized as part of the embryo, this embryo will be more or less perfect according as the needle thrust has destroyed more or less and even according as it has destroyed one-part or another of the cell, for thus the dead part will come to occupy a ventral or a dorsal position, etc., in the embryo.

This description of the formation of embryos that are more or less complete, according as the mass of inert substance is less or greater, is strongly opposed to the conception of Roux that, namely, the half egg first formed a half embryo. Yet Roux allowed that a more complete embryo was *subsequently* formed from the half by a process of revivification of the inert half, by what he called postgeneration. The ultimate result is thus the same according to either investigator.

Moreover Hertwig concedes that some process of "postgeneration" takes place to convert part of the inert mass into active cells; the injury to the cell having been in part but temporary so that it may later take part in forming the embryo.

While Roux insists upon the power of one cell to develop by itself as a half embryo and then to coerce the inactive half into the subsequent formation of the complete embryo, Hertwig lays stress upon the continuity and uniformity of a process that is from the first a formation of a whole embryo by the half-egg, subsequently, in part, assisted by the slow acting injured half.

With an omission of a critique upon Roux's conceptions of developmental processes we pass to the general conclusions that end the paper

Pressure that changes the shape of the amphibian egg induces great changes in the directions and sequence of the cleavage planes and in the size of the cells.

The direction of the planes results from the form of the cell and the distribution of its protoplasm.

There is no causal connection between the first planes and the axes of the body; the main axis of the body is not determined by the position of the first or second cleavage planes.

In the various induced forms of cleavage the nuclei that are formed become, in the different cases, distributed to very various parts of the yolk; they may be vicariously distributed to all parts of the yolk.

As, the cleavage does not separate parts of the yolk predestined to form definite parts of the animal, so also the nuclei are not qualitatively divided into different kinds of nuclear material for the various cells. Yet normal embryos with normally placed organs arise from such mixed up or unnaturally distributed nuclei.

The egg contains no definite substance set apart to form special organs (liver-, skin-, retina-forming material) but it is isotropic. The contents of the egg ceases to be isotropic and becomes more and more specialized and organized in the process of cell multiplication with its important chemico-physical transformations (such as increase in the nuclear material).

In spite of this isotropy the egg is a definitely organized cell with yolk, protoplasm, etc., of different specific gravity.

This specific nature of the egg contents and also the shape of the egg exercises a directive influence over the process of development; the embryo at first must be adapted to the form of the egg.

The shape and position of the egg determine the position of the first cleavage planes.

As no rearrangement of heavy and light portions takes place in cleavage the distribution of mass in the egg corresponds to that in the blastula.

When the walls of the blastula are not uniform the gastrulation can take place only in a special zone which is below the equator when there is less yolk, as in the amphibian egg, and above when there is very much yolk, as in meroblastic eggs.

From an oval or elongated egg there is formed an elongated blastula, gastrula, etc. (in triton and insects, etc.).

As many eggs have elso a bilateral arrangement of their component substances there must follow a bilateral blastula in which the place for formation of the blastopore will be more sharply defined.

The chief axes of the embryo may correspond approximately to the first cleavage planes in eggs that are bilaterally symmetrical or that have one long diameter, since the character of the egg determines both.

In the gastrulation of the amphibian egg there is a revolution about an axis cutting the plane of symmetry and the plane of equilibrium.

Eggs of complex consistency are acted upon by gravitation so that they are oriented and if bilaterally symmetrical stand with the plane of symmetry vertical since this is also the plane of equilibrium.

If such eggs are forced to develop in a constrained position they form asymmetrical embryos so that gravitation is, in a sense, one of the influences determining structure.

If one of the first two cells of the egg is destroyed the other develops into a tolerably normal embryo having, however, some of its less important regions defective.

When one cell is but partly destroyed it may later form cells that are added to the uninjured half to help form the embryo. This secondary formation of cells in the injured half may be from the uninjured nucleus of that cell, or sometimes, by the migration of nuclei from the uninjured egg-half into the injured egg-half.

The development of the uninjured half, by itself or with the aid of part of the injured half, follows the same laws as the natural ontogeny of the species.

The injured yolk acts in the development of this half of the egg as the nutrient material does toward the formaitive in a meroblastic egg.

The process of postgeneration described by Roux does not take place nor is there a revivification of the destroyed egg-half.

Embryos with cleft blastopore cannot form double monsters by the process of postgeneration that Roux brought in to explain such a formation.

We cannot form at will half-anterior, -posterior or -lateral blastulas or embryos by destroying one of the first two cleavages cells.

In these cases of injury complex processes of adjustment may result in the formation of a normal embryo under changed circumstances.

The results obtained by these pressure experiments as well as the injury to one of the cleavage cells demonstrate the untenability of the mosaic theory, the theory of specialized germ areas and Weismann's theory of germ plasm.

The egg is a specifically organized one-celled organism that develops epigenetically by process of multiplication of cells with subsequent differentiation.

Since each cell comes from the first (the egg) by division it likewise contains the beginnings of the whole and becomes differentiated and specific during process of development according to the position it occupies in the whole at any period (gastrula, etc.). The reasons leading up to this position may be put under the following seven heads: 1. A complete organism may be formed from one of the first two or four cells; accordingly in different cases cells of like origin must be put to forming different organs. 2. As the gastrula mouth may appear at various parts of the periphery the cells concerned must have different ates in different cases. 3. The same is true in the abnormal cases of formation of multiple gastrula mouths; then there may be formed four instead of two eyes, ears, etc. 4. Frog's eggs that develop when held up-side-down must have the material utilized in a different way from the normal. 5. Thus also the triton larvæ show various ways of using the similar cells when the first two are partly separated by a thread. 6. When the frog develops up-side-down cases occur in which the lip of the blastopore is rolled outward and unites with the other lip so that the line of union is not between the edges of the lips but between the edge of one and the turning out surface of the other. Then the notochord and the medullary plate would be formed from cells quite other than those normally acting. 7. Changes in the cleavage process that so mix up the nuclear substance that it is assigned to different parts of the yolk in different eggs have no influence upon the normal result of development.

Thus in place of the mosaic theory of Roux and the germ-plasm theory of Weismann we may substitute the theory of the controlling inter-adjustments of the embryonic cells and later of the tissues and organs.